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Investigating whether light intensity can modify decomposition rates in peatlands through control of the 'enzymic latch'

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ABSTRACT

Root exudates released by vascular plants contain significant amounts of photosynthetically-derived low molecular weight carbon compounds and gases, such as oxygen. These compounds are reported to have a priming effect on the activity of soil microbes which, in turn, release extracellular soil enzymes. Rates of root exudation are known to correlate positively with photosynthesis rates. As such, we hypothesized that phenol oxidase activity in the rhizosphere of peatland plants could be manipulated by varying the intensity of light to which above ground biomass is exposed, in line with recent solar radiation management proposals of geoengineers. Since phenol oxidase plays a pivotal role in regulating biodegradation in peat soils, through a mechanism widely known as the 'enzymic latch', this approach was thought to have potential as an ecoengineering strategy designed to enhance carbon sequestration in these environments. Our experiment however, found little relationship between phenol oxidase activity and light intensity level for any of the plants analysed, although significant differences in enzyme activity were observed between plant species. It is argued therefore, that encouraging the growth of particular plant species may be more effective at enhancing carbon sequestration in peatlands than manipulating ambient light levels.

1. Introduction

Peatlands have sequestered vast stores of carbon over millennia due, primarily, to the accumulation of partially decomposed organic matter in anoxic soils (Clymo, 1984) and it is estimated they continue to do so at an average rate of 0.05, to 0.096 Pg (1 Pg = 10^{15} g) of carbon per year (Yu et al., 2010; Clymo et al., 1998; Gorham, 1991). Decomposition of some soil organic matter (SOM) does take place in peatlands though – to varying degrees – releasing carbon in aqueous (dissolved organic carbon, DOC), solid (particulate organic carbon, POC) and gaseous forms such as carbon dioxide (CO_2) and methane (CH_4; Freeman et al., 2001a,b; Gorham, 1991; Worrall et al., 2003). The flux of these latter two key greenhouse gases (GHGs) between peatlands and the atmosphere has a significant effect on the Earth's climate. Globally, these wetlands currently act as a net sink for atmospheric CO_2 (Kayranli et al., 2010) and crucially, unlike other ecosystems (such as forests) they are potent long term repositories for this carbon (Dunn and Freeman, 2011; Freeman et al., 2012; Holden, 2005). The actual mechanism allowing this carbon accretion, the 'enzymic latch' (Fenner and Freeman, 2011; Freeman et al., 2001b), is so called because the sequestration results from a suppression of the normal enzymic decomposition pathways. This unusual stalling of SOM breakdown is the result of a disproportionate concentration of enzyme-inhibitory phenolic compounds in the peat-matrix. These accumulate due to constraints on phenol oxidase enzymes (Freeman et al., 2001b) which impede activities of the major agents of decomposition; namely, hydrolase enzymes (Freeman et al., 2004). Removal of these limitations on phenol oxidases, such as oxygen availability, temperature and pH, can initiate a biogeochemical cascade of degradation (Fenner and Freeman, 2011; Freeman et al., 2001a, 1997, 2004). Conversely, manipulation or strengthening of this enzymic latch has the potential to promote enhanced peatland carbon sequestration (Freeman et al., 2012). Such amplified suppression of decomposition in peat-soils would increase SOM accumulation, maximise the carbon storage intensity per unit area of peatlands and offer a new approach to geoengineering – acting as a cost efficient CO_2 removal (CDR) scheme (Royal Society, 2009). We propose one method for doing this involves altering the amount of light available for photosynthesis to peat-

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land plants. Preventing optimal rates of photosynthesis would decrease root exudation and thus further lower phenol oxidase activity in the rhizosphere.

Root exudation is part of the rhizodeposition process of plants and involves the release of ions (eg. H^+), inorganic acids, oxygen, water and a wide-variety of carbon-based compounds, depending on the species of plant and its age, along with external factors such as biotic and abiotic stresses (Badri and Vivanco, 2009; Bais et al., 2006). Known as the 'rhizosphere priming effect' (RPE; Kuzyakov, 2002) these rhizodeposits are known to affect microbial communities and their activities in the soil surrounding the roots (Shackle et al., 2000) – an area known as the rhizosphere. Amplified rhizodeposition has been shown to increase microbial activity in the rhizopshere (Oger et al., 2004), and as most phenol oxidases in peat-soil are produced by bacteria (Burke and Cairney, 2002) and fungi (Thormann, 2006; Fenner et al., 2005), it is likely these enzymes will be affected too. Previous studies have shown that increased rates of photosynthesis increase rhizodeposition (Graham et al., 1982; Rovira, 1969); therefore by repressing photosynthetic activity, by altering the amount of light reaching peatland plants, it may be possible to curtail microbial activity and the production of phenol oxidase. The enzyme's activity may also be suppressed under sub-optimal photosynthesising conditions due to increased soil hypoxia, as oxygen (essential for phenol oxidase activity) is also a common root exudate (Bertin et al., 2003). The release of oxygen from the roots of some wetland plants, known as radial oxygen loss (ROL) has been shown to be correlated to photosynthetic activity (Lai et al., 2012). We hypothesise that higher rhizodeposition will lead to higher extracellular phenol oxidase activity.

The intensity of the light, or photon flux density (PFD), which promotes optimal rates of photosynthesis, is different depending on the plant species. Increasing the PFD beyond this point results in photosynthetic saturation, as the rate of photosynthesis does not increase, and eventually photoinhibitory damage, due to the over excitation of the photosynthetic reaction centres (Björkman and Demmig-Adams, 1994). It was not known what the optimal PFD for photosynthesis was for the two vascular plant species used in our study so 750 μmol m^{-2} s^{-1} was selected as it was the average light intensity during the growing season at the chosen blanket bog site in North Wales, UK (personal communication, CEH 2013).

Being a dominant peatland plant, the effect of light on *Sphagnum* mosses was also investigated. As bryophytes, they do not have roots in the same way as vascular plants, however; they do exude organic carbon which can increase microbial activity in the peat-soil (Fenner et al., 2004; Shackle et al., 2000). And with bryophytes being generally shade-loving plants (Davey and Rothery, 1997), it was hypothesised that phenol oxidase activities would be highest in bryophytic plants grown under lower light conditions, as they would reach photosynthetic saturation, or even be affected by photoinhibitory damage, at higher PFDs.

To investigate how varying the light intensity would affect phenol oxidase activities in the rhizosphere of peatland plants through rhizodeposition, intact peat mesocosms were collected from a blanket bog in the UK and grown for six weeks under experimental conditions in a specially constructed growth room. If it was discovered that altering the PFD reaching peatland plants could increase the levels of carbon sequestered by peatlands, it would require methods to shade or intensify vast areas of land. However, as an ecoengineering or 'geoengineering' project this may not be inconceivable, in terms of physical practicability and/or expense, when compared to other Solar Radiation Management (SRM) methods currently being considered. These include increasing the albedo of the desert, stratospheric aerosols and even the manufacture and release of space-based reflectors (Royal Society, 2009). Indeed one of the unintended consequences of some SRM projects may be a reduction in the Photosynthetically Active Radiation (PAR) reaching peatlands, creating the potential for additional carbon sequestration through a lowering of rhizospere priming.

2. Methods

Mesocosms of peat-soil (22,800 mm^2 × 220 mm) and vegetation, were collected at the start of the summer from the Migneint Valley in North Wales, UK. The area is a 200 km^2 Special Area of Conservation, incorporating one of the largest areas of blanket bog in Wales. The area is 460 m above sea level and is predominantly a *Sphagnum*-rich, *Calluna vulgaris* (common heather) and *Eriophorum vaginatum* (hare's-tail cotton grass) dominant blanket mire, with acid grasses on drier hillslopes, and *Juncus effusus* (soft rush) in riparian areas. The underlying geology of the ombrotrophic bog is a mixture of acid and basic volcanic rocks, Ordovician shales and mudstones. Annual rainfall is 2400 mm and in the peat the water table is usually within 100 mm of (and often at) the ground surface. The study area has a pore water pH, at a depth of 100 mm, in the range of 4.1–5.1. The mean peat depth across the site is 2000 mm (Evans et al., 2012).

The mesocosms (held within black plastic containers) were collected so that they were dominated by one of the three experimental vegetative species – according to a score of 5 on the Braun-Blanquet cover-abundance scale (Wikum and Shanholtzer, 1978). The species studied were mixed *Sphagnum* moss species, *Calluna vulgaris* and *Eriophorum vaginatum*: referred to as *Sphagnum*, *Calluna* and *Eriophorum* (respectively) throughout this study. All groups of mesocosms containing one of the species were taken from an area of approximately 25 m^2 and the entire study area was approximately 100 m^2.

Using one of the plastic containers with both ends removed as a guide each monolith was carefully extracted, to ensure the surface vegetation was kept intact and compaction of the soil was avoided to prevent any changes to its physical structure.

Once the mesocosms had been collected (a total of 45, consisting of 15 *Sphagnum*, 15 *Calluna* and 15 *Eriophorum*) they were returned to the laboratory, approximately 30 miles from the study site. They were placed in a climate controlled room (set to 18 °C) with commercially available growth lights, set to give 12 h conditions of 1000 (±20) μmol m^{-2} s^{-1} PAR and 12 h of darkness, for one week (a Techone 600 w Energy Saving Digital Electronic Ballast fitted with a high pressure sodium a dual spectrum lamp). Soil samples were taken, 4 g, from a depth of 50 mm within the mesocosms, using a 10 mm soil-borer and taking care to minimise any disturbance to the vegetation or soil structure.

The mesocosms of each species were then split into three groups randomly assigned a light regime (with $n = 5$) for the next six weeks which meant they were either kept under the full 1000 (±20) μmol m^{-2} s^{-1} PAR conditions, or they were shaded – using horticultural mesh – so they received 750 (±20) μmol m^{-2} s^{-1} PAR or 500 μmol m^{-2} s^{-1} PAR (Fig. 1). The levels of PAR were measured using a LI-250A Light Meter, from a set point above the mesocosms regularly throughout the experiment. All other conditions were kept the same. Water levels in the mesocosms were checked daily and kept consistent with the level of the water table in field at time of collection, using laboratory prepared distilled water.

The activity of extracellular phenol oxidases in the peat-soil from the different mesocosms was determined every week using 10 mM L-DOPA (dihydroxy phenylalanine) (Sigma-Aldrich Co., Ltd, Dorset) solution as a substrate, based on the procedure of Pind et al. (1994), Williams et al. (2000) and Dunn et al. (2014). Peat samples for the analyses were taken randomly from a depth of 5 cm from every mesocosm.

The concentration of water extractable phenolics from the peat samples were assayed every week using a modified version of the

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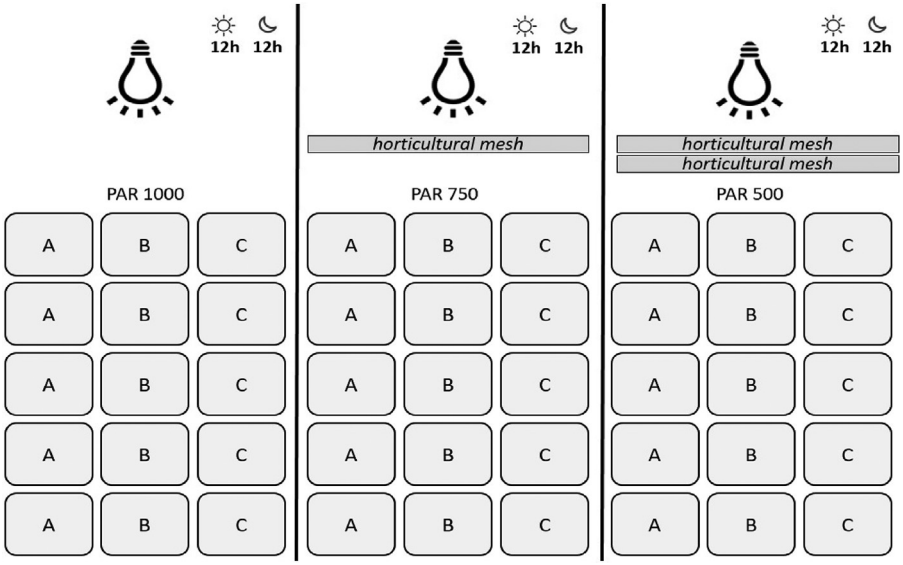

Fig. 1. Setup of experiment with mesocosms (grey boxes) containing A = *Sphagnum* species; B = *Eriophorum*; C = *Calluna*. PAR values presented in μmol m^{-2} s^{-1}.

spectrophotometric method developed by Box (1983). It has been suggested that there is no single optimal protocol for quantification of total phenolic concentrations (Yu and Dahlgren, 2000). However, we selected the Folin-Ciocalteau method because it has been shown to be superior to most other methods (Yu and Dahlgren, 2000) and has been used previously for similar peat-soil samples (Fenner et al., 2005; Freeman et al., 2004). Although the method may have limitations (Yu and Dahlgren, 2000), because we ensured the same extraction and quantification methods were applied to all peat samples, comparisons should prove reliable.

Relationships between variables were measured using Pearson's correlation coefficient (r), while significant differences between results were determined by independent one-way analysis of variance (ANOVA) tests and repeated measure ANOVAs. All statistical tests were performed using PASW Statistics 18 (currently IBM SPSS; IBM Corporation, New York, USA).

3. Results

The results from Fig. 2 and analysis using repeated measures ANOVAs suggest that for all three plant species investigated there were no statistically significant differences on the effect of light intensity on phenol oxidase activity over the six week experimental time period (Fig. 2): *Sphagnum*, F (8.16, 48) = 1.448, p = 0.207; *Eriophorum*, F(9.22, 36) = 1.797, p = 0.105; *Calluna*, F(10, 48) = 1.545, p = 0.153. There was also no significant differences, for any of the species (*Sphagnum* (F (2, 14) = 2.601, p = 0.115)); *Eriophorum* F (2, 5.9) = 3.056, p = 0.123; *Calluna* (F (2, 14) = 0.453, p = 0.646), when only the final week's enzyme activities were taken into account for each of the three light intensities. However, when all the weekly results were combined for the respective plant species and light intensity groups (Fig. 3), a series of one-way ANOVAs indicated that there was statistically less phenol oxidase activity in the rhizospheres from the *Calluna* mesocosms at 50% full light (M = 0.03 μmol dicq g^{-1} min^{-1}, SE = 0.004), compared to those under full light conditions (M = 0.05, SE = 0.007): F(2, 64.35) = 5.157, p = 0.008, with a relevant planned contrast of t (64.49) = −1.170, p = 0.004.

The light treatments only changed the final phenol oxidase activity in the rhizosphere of the *Calluna* mesocosms, with all the samples showing a decline (F (3, 12.5) = 13.488, p < 0.001), com-

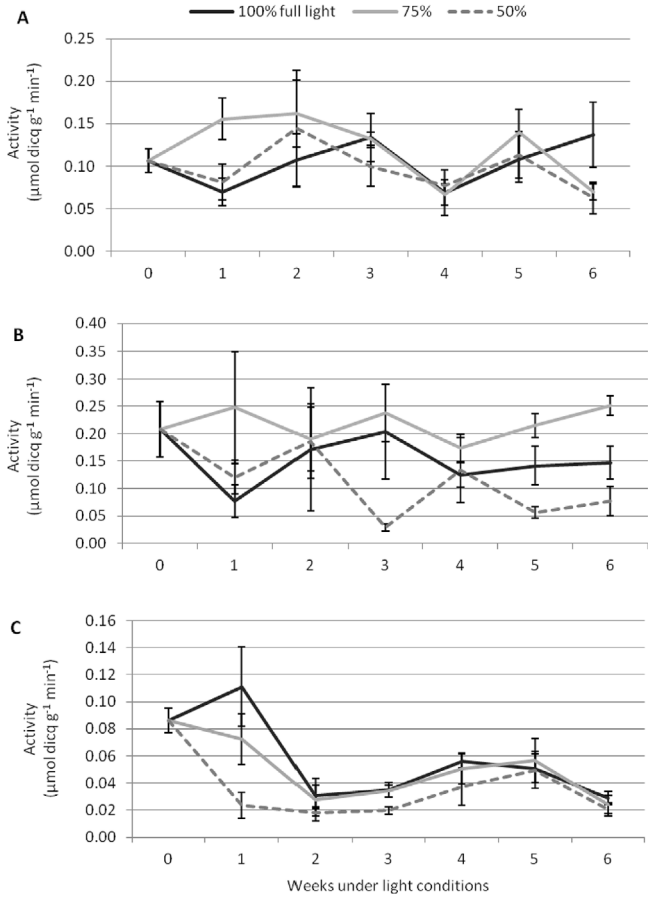

Fig. 2. Phenol oxidase activity in the rhizosphere of different peatland plant species over a six week period under varying light conditions. Peat-soil samples taken from a depth of 5 cm from mesocosms containing **A** = *Sphagnum* species; **B** = *Eriophorum*; **C** = *Calluna*. Mean averages are shown (n = 5) and error bars indicate ± standard error. The different scales of the y-axes, and initial activities, should be noted when making comparisons.

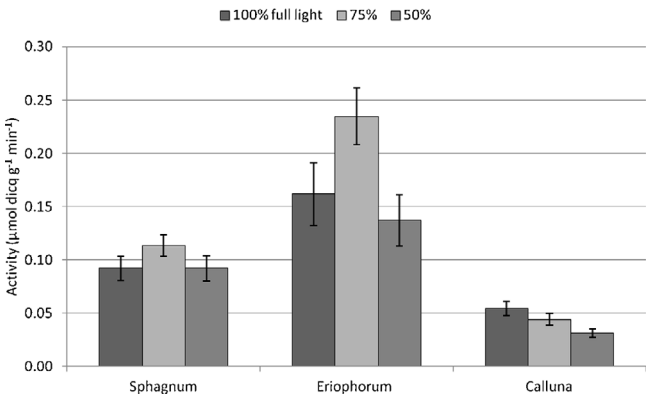

Fig. 3. Phenol oxidase activity in the rhizosphere of peatland plant species. Mean averages from the entire six week experiment are shown ($n = 35$). Error bars indicate ± standard error.

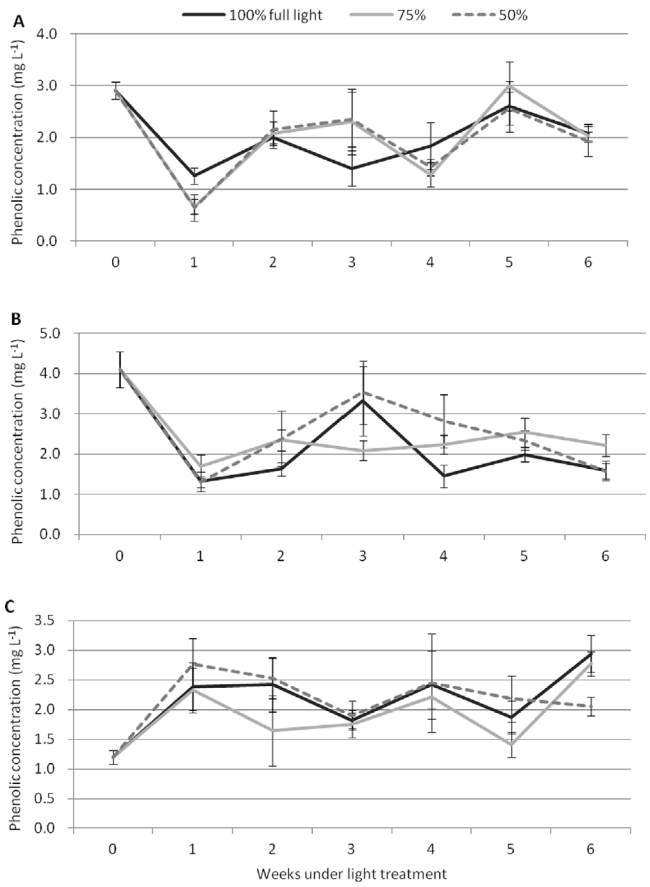

Fig. 4. Water extractable phenolic compound concentrations (mg L^{-1}) from the rhizosphere of different peatland plant species over a six week period under varying light conditions. Peat-soil samples taken from a depth of 5 cm from mesocosms containing **A** = *Sphagnum* species; **B** = *Eriophorum*; **C** = *Calluna*. Mean averages are shown ($n = 5$) and error bars indicate ± standard error. The different scales of the y-axes, and initial concentration levels, should be noted when making comparisons.

pared to before the light treatments were administered. In both the *Sphagnum* and *Eriophorum* mesocosms, activities remained statistically unaltered after six weeks.

Water extractable phenolic concentrations from the rhizospheres of the different plant groups were also not affected by light intensity, with all three intensities showing no significant difference from each other over the six weeks (Fig. 4): *Sphagnum*, $F(9.77, 46) = 0.837$, $p = 0.594$; *Eriophorum*, $F(8.93, 48) = 1.887$, $p = 0.081$; *Calluna*, $F(9.55, 48) = 0.612$, $p = 0.789$. There were also no significant

Table 1
Water extractable phenolic concentrations (mg L^{-1}) in the rhizosphere of peatland plant species. Mean averages from the entire six week experiment are shown ($n = 35$) in bold. Error bars (in parentheses) indicate ± one standard error.

	Sphagnum	Eriophorum	Calluna
100% full light	**1.990** (0.138)	**2.163** (0.215)	**2.119** (0.160)
75%	**2.002** (0.176)	**2.606** (0.265)	**1.917** (0.140)
50%	**2.042** (0.176)	**2.605** (0.255)	**2.171** (0.165)

differences, for any of the plant species, when the mean average of the phenolic concentrations (over the six week time period) were taken into account for each of the three light intensities (Table 1). Unlike, the enzyme results though all the samples taken from the plant groups, irrespective of the intensity of the light they received, showed a significant change in phenolic concentration at the end of the experiment, compared to the start. Data from Week 0 and Week 6 indicated that phenolic concentrations in the *Sphagnum* ($F(3, 26) = 6.134$, $p = 0.003$) and *Eriophorum* ($F(3, 24) = 8.226$, $p = 0.001$) rhizospheres all declined after six weeks, while they increased in the *Calluna* ($F(3, 26) = 23.62$, $p < 0.001$) samples.

When the phenol oxidase activity of all the plant species from the final week of the experiment (week six) were grouped together and plotted against their relevant phenolic concentrations (Fig. 5), there was a statistically significant negative correlation for those mesocsoms kept in 100% light and those kept in 75% light ($r = -0.69$, p (one-tailed) = 0.005, and $r = -0.608$, p (one-tailed) = 0.018, respectively), albeit of a moderate size. There was no statistically significant correlation between phenol oxidase activity and phenolic concentrations at 50% full light: $r = -0.395$, p (one-tailed) = 0.073.

By amalgamating all the weekly results for peat-soil phenol oxidase activity for each plant species under the separate light intensity treatments, differences between species were identified (Fig. 3). At 100% full light there were statistically significant differences between the species ($F(2, 55.9) = 9.161$, $p < 0.001$), and post hoc comparisons, using the Games-Howell test, revealed that the enzyme activity in the rhizosphere of the *Calluna* mesocosms were significantly less than the *Sphagnum* ($p = 0.016$) and *Eriophorum* ($p = 0.003$) samples. Both the other two light treatments, 75 and 50% full light, showed the same effects ($F(2, 50.73) = 30.099$, $p < 0.001$ and $F(2, 48.78) = 19.391$, $p < 0.001$, respectively) with the former also indicating that *Sphagnum* samples had significantly less phenol oxidase activity than those from the *Eriophorum* mesocosms ($p < 0.001$). When phenolic concentrations (Table 1) were analysed in a similar way, no significant differences were observed between species.

4. Discussion

It has long been accepted that light intensity affects vascular plant root exudates into the rhizosphere. Higher light levels, and the associated higher rates of photosynthesis, generally result in increased rhizodeposition (Graham et al., 1982; Rovira, 1969) including the release of CO_2 (Kuzyakov and Cheng, 2001) and oxygen (Christensen et al., 1994; Sorrell, 1999). As root exudates can substantially increase microbial activity in the rhizosphere (Oger et al., 2004; Shackle et al., 2000) it was hypothesised that when light levels were optimal for photosynthesis by the species, production and release of phenol oxidases would increase from the communities of bacteria (Fenner et al., 2005) and fungi (Burke and Cairney, 2002) and even from the plants themselves (Gramss et al., 1999). When coupled with root oxygen release, raising the redox

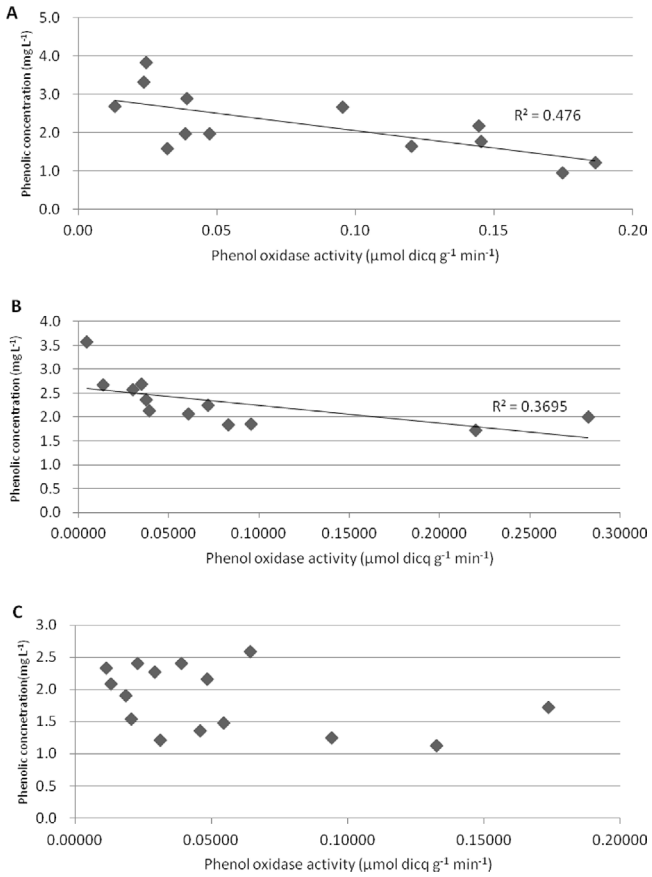

Fig. 5. Investigating the relationship between phenol oxidase activity and water extractable phenolic compound concentrations from the rhizosphere of a blanket bog under varying light conditions. Peat-soil samples taken from a depth of 5 cm from mesocosms containing *Sphagnum*, *Eriophorum*, and *Calluna* species. Data for all species, from week six, are shown in each graph. **A** = 100% full light; **B** = 75% full light; **C** = 50% full light. The different scales of both the y- and x-axes should be noted when making comparisons.

potential of the soil, these conditions would increase the enzyme's measurable activity in the peat-soil by 'opening' the enzymic latch (Freeman et al., 2001b). The same was predicted in the mesocosms containing *Sphagnum* species, as although being bryophytes and not having roots like higher plants, *Sphagnum* species are also known to exude organic carbon which can increase microbial activity in the peat (Fenner et al., 2004). However, our results showed that the only significant effect photon density had on phenol oxidase activities were found when the mean average of the whole six weeks was considered, with *Calluna* samples at 50% full-light showing a 43% drop in activity compared to those at 100% full-light (Fig. 3).

Otherwise there were no significant differences in the enzyme's activity between the photon density treatments for any of the plants over the experimental time period. This could indicate that none of the range of light levels we used were optimal for photosynthesis in any of the species, although this is not possible to conclude conclusively without photosynthesis and accurate growth rate data, but it should still have been possible to identify differences between those samples at full light (250 μmol m^{-2} s^{-1} above the equivalent of a bright sunny day) compared to those shaded and only receiving 50% full light (or 250 μmol m^{-2} s^{-1} less than a sunny day). It may have been possible that light treatments were actually having an effect on rates of photosynthesis and root exudation levels, but any effect on phenol oxidase activity was offset by a correlated release of phenolic compounds, exuded from the roots of the *Calluna* or *Eriophorum* (Dakora and Phillips, 2002) and *Sphagnum* tissues (Rasmussen et al., 1995). These inhibitory chemicals would have suppressed the activity of hydrolase enzymes and the further release of inorganic nutrients needed by phenol oxidase-producing microorganisms (Fenner and Freeman, 2011). However, this explanation seems unlikely as we did not observe any significant differences in leachable phenolic compound concentrations for the light treatments in any of the plant species (Fig. 3 and Table 1).

Calluna was the only species to show an overall decline in phenol oxidase activity over the six week experimental time period (Fig. 2), corresponding with an overall increase in leachable phenolic compound concentrations (Fig. 4). This could be due to the observed structure and morphology of *Calluna* roots, the roots hairs of which were at a greater depth than *Eriophorum* or *Sphagnum*. Therefore any increase in phenol oxidase activity may: 1) not have been measurable with our sampling regime and 2) been suppressed by increased anaerobic conditions found at greater depths in the peat-soil profile. Indeed, average phenol oxidase activities were found to be lower in all the *Calluna* samples compared to the other two plant species investigated (Fig. 3).

To answer the main question of our study, our results suggest that light intensity does not universally regulate phenol oxidase activity in the rhizosphere of a blanket bog. Interestingly though we did observe significant differences in the enzyme activity between the plant species themselves. For all light regimes, *Eriophorum* had the higher phenol oxidase activities, followed by *Sphagnum* and then *Calluna* (*Eriophorum* > *Sphagnum* > *Calluna*). If phenol oxidase activity is used as a proxy for the decomposition of organic matter, and thereby release of both gaseous (CO_2) and aqueous (dissolved organic carbon, DOC) carbon from peatlands (Freeman et al., 2004), our results suggest that *Calluna* (heather) is the most desirable plant species to maximise the ecosystem's carbon sequestration capabilities. With lower phenol oxidase activities allowing the build-up of hydrolase enzyme-inhibitory phenolic concentrations (Fenner and Freeman, 2011).

Before conclusions are drawn about the potential of altering light-densities across areas of peatland for geoengineering projects, further interdisciplinary research should be undertaken to continue the work of this pilot study. For instance, rates of photosynthesis must be measured, and a wider range of photon densities should be used including going lower than 500 μmol m^{-2} s^{-1} and higher than 1000 μmol m^{-2} s^{-1}, in order to determine where each wetland plant species has its maximum and minimum photosynthetic rate and where they reach photosynthetic light saturation. It should also be investigated as to whether the use of horticultural mesh affected the spectrum of light reaching the plants. Other factors such as temperature and vapour pressure (Goodrich et al., 2015) may also be having an effect on controlling photosynthesis and these should be monitored and accounted for in any future experiments. It's possible that light is not the main driver controlling photosynthesis and this may therefore account for the lack of a clear relationship between light and phenol oxidase activity.

Alongside phenol oxidase and phenolic compound concentration measurements, carbon pathways must also be analysed from the samples with regular CO_2 fluxes and DOC measurements being taken.

Our results do provide support for the use of the enzymic latch mechanism to supress organic matter decomposition in peatlands, with the significant negative correlations between phenol oxidase activities and leachable phenolic compound concentrations observed for 100% and 75% full-light treatments, when the results of all the plant species were amalgamated (Fig. 5). These observations are consistent with previous work, which looks at the relationship between phenolic compounds and phenol oxidase (Fenner and Freeman, 2011; Freeman et al., 2001a,b, 2004) and confirms that when phenol oxidase activity is low phenolics accumulate.

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Therefore, our study suggests the most promising application of peatland plants, if they were to be used in an ecoengineering or geoengineering project, would be to selectively encourage the growth of certain species in order to minimise the activity of phenol oxidases in the peat soil as supported by Dunn et al. (2016). We would suggest the order of peatland plants to achieve maximised suppression of organic matter decomposition is therefore; *Calluna* > *Sphagnum* > *Eriophorum*.

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